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V.

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY
OF THE MUSEUM OF COMPARATIVE ZOÖLOGY
AT HARVARD COLLEGE.

No. IV.—THE EXTERNAL MORPHOLOGY OF THE LEECH.

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Communicated June 11th, 1884, by Alexander Agassiz.

THERE is no invertebrate animal about which more has been written than about the Medicinal Leech ; but, as Dalyell long ago remarked, "it does not appear that the history of the leech has advanced in proportion to the number of the *literati* who have rendered it the subject of discussion." As a considerable share of the work done in this direction is purely systematic, it is somewhat surprising that not a single description of any *Hirudo* has been given with sufficient accuracy and completeness for a close comparison of even its more important external characters with those of other species. More than this, it would be impossible, from the many monographs, memoirs, and stray papers devoted to this subject, to patch up a description that would fully meet the requirements for a critical comparison of any two species. By far the greater number of species-diagnoses that have been showered upon us from time to time have been so superficially and slovenly done, that it would probably puzzle the perpetrators to identify the species they profess to have described. Some of the more important diagnostic characters have been either entirely ignored, or given with such vagueness that they are of little service in identification, and absolutely worthless for comparative purposes. No uniform mode of counting the rings has been adopted ; and, judging from the descriptions themselves, systematic writers have, for the most part, failed to place much value on the rings in the determination of species and genera. No one appears to have suspected the existence of segmental sense-organs in the leech ; much less the serial homology of the eyes with such organs. It is the object of this paper to make clear both these facts ; and, at the same time, to show that the rings and somites form the only proper basis of classification. The latter fact will be brought out by a comparison of a few well-marked genera.

It is a well-known fact that the end somites are *incomplete* in respect to the *number* of rings composing them; but the mode and extent of abbreviation have not hitherto been made the subject of careful study; and hence some of the more important generic characters have been entirely overlooked, and with them some points of the highest morphological interest. *Hirudo* is the best known and most widely distributed genus, and on this account forms a convenient standard of comparison. As the arrangement of the segmental sense-organs enables us to determine the exact number of somites composing the body, we may deal with this part of our subject first.

The Segmental Sense-organs of the Leech. — The only sense-organs hitherto known in the Medicinal Leech are the five pairs of eyes and the so-called "goblet-shaped" organs located on the lip (cephalic lobe). A number of writers have noticed and described some small spots, occurring on every fifth ring of the body; and one author has suggested that they may have a respiratory function. These spots when examined closely with a low magnifying power will be found to be slight elevations with rounded summits; and for this reason, and because they are regularly disposed on the first ring of each somite, they may be called *segmental papillæ*, a name which does not prejudice the question of their function.

In our large Pond Leech (*Macrobdella* Verrill), these papillæ are comparatively small; and the same may be said of the medicinal leeches of Europe and Japan, and their nearest allies, *Hæmopsis* and *Aulostoma*. In some of the Asiatic medicinal leeches, for example, those of Saigon, Singapore (*H. maculosa*), Java (*H. javanica*), and Ceylon (*H. multistriata*), they are much larger, and have an oval form, with a median ridge or crest. In the land leeches they are very conspicuous, having the form of small cones with rounded summits.

In all the ten-eyed leeches of Japan, including both the land and fresh-water forms, twelve of these papillæ are found on the first ring of each complete somite, six on the dorsal and six on the ventral side. In most of the medicinal leeches, however, as well as in *Hæmopsis*, *Aulostoma*, *Macrobdella*, etc., there are eight on the dorsal side, and six on the ventral.

A careful study of the arrangement of these papillæ in a large number of species, and of their histological structure, has brought out in a most conclusive manner their serial homology with the eyes; and has led, indirectly, to the recognition of some important points in regard to the metameric composition of the body of the leech. The arrangement of the papillæ on the dorsal side is shown in Fig. 1.

The eyes are represented by five pairs of large black dots; the papillæ, by smaller dots. The numerals on the left of the diagram give the number of somites; those on the right, the number of the first ring of each somite. The position of the seventeen pairs of nephridial pores is shown by short dashes (1st *p* to 17th *p*). With the exception of the genital and nephridial pores, the diagram shows only what belongs to the dorsal side.

It will be seen that there are twenty-six transverse rows of papillæ, — one for each somite; and that, owing to their uniform and symmetrical arrangement, they form also *eight longitudinal rows*. We have *two median* rows (*m*) formed of twenty-five successive pairs; *four lateral* rows, an *inner* (*il*) and an *outer* (*ol*) on each side of the median line; and *two marginal* rows (*mg*). The first two eyes hold the position of a pair of median papillæ, while the remaining eyes replace as many *inner lateral* papillæ. About this correspondence in position there is not, in my opinion, any room for doubt. In the diagram the outer lateral and marginal papillæ are to be seen as far forward as the first eye-bearing ring, the marginal ones alone being absent on this ring; but in most species of *Hirudo* both of these rows of papillæ are very indistinct, or entirely absent on the first three eye-bearing rings. They are present in *Aulostoma*, and are very distinct in the large medicinal leeches of Saigon, Singapore, Java, and Ceylon.

The median rows of papillæ, if their position is not misleading, must be regarded as the metameric equivalents of the *first* pair of eyes; the inner lateral rows hold the same relation to the 2d, 3d, 4th, and 5th pairs of eyes. There is a possibility that the first pair of eyes are derivatives of the inner lateral papillæ, the median papillæ of this ring having been lost, and the eyes brought nearer together so as to stand in line with the median papillæ of the following somites. However, as all the papillæ have the same structure, there is no objection on this score to the opinion that the eyes are derived from both the median and the inner lateral papillæ.

The structure of the papillæ confirms the homology above indicated, if one feature alone be excepted. The eye of the leech, as is well known, is a cylindrical mass of cells, three or four times as long as wide. The central or axial portion is made up of peculiar large glassy cells, in general appearance entirely unlike the other cells of the body. What the peculiarities of these cells are cannot well be explained without illustrative drawings; but, for present purposes, it will be sufficient to say that each of these cells has a vacuole-like central space, which is probably filled with some kind of fluid. What-

ever this fluid may be, it is not stained by any of the dyes in common use. The protoplasm of these cells forms a thick peripheral layer, with a rounded thickening at one point, which projects into the vacuolar space. The very small nucleus is usually located near the base of the internal protuberance.

The axial portion, consisting of glassy cells, is enveloped by a thick layer of pigment on all sides except the external end. The epidermal cap covering these cells is convex and entirely free from pigment, forming thus a window-like opening into the black pigment-cup which holds the large clear cells. An optic nerve enters the eye near its deeper end, and runs along the axis for a larger portion of its length. It is probable that branches of the nerve connect with the clear cells; but precisely how has not been ascertained.

In sections of the segmental papillæ, we find all the elements of the eye, except the pigment. There is a branch of the lateral nerves that runs to each; and from four to six or more of those large glassy cells are found a little below the epidermal cap, which is convex and free from pigment. The absence of a pigment-cup holding the glassy cells makes it doubtful whether the papillæ can be regarded as visual organs; but it does not, to my mind, weaken the evidence of their serial homology with the eyes.

It is generally found that the posterior eyes, especially the fifth pair, are smaller than those preceding them; and I have noticed cases in which only a mere trace of pigment could be seen in one or both of the last pair of eyes. While it appears doubtful what the special function of the papillæ is, still the presence of large clear cells, precisely like those in the eye, situated just below the window-like opening in the surface pigment, and their obvious serial equivalence with the eyes, makes it not improbable that they represent incipient organs of vision.

Although the evidence appears to me conclusive that the eyes and the segmental papillæ were, originally, morphological as well as physiological equivalents, it does not, of course, follow necessarily that both organs now have the same functional significance. The original papillæ may have represented sense-organs of a more or less indifferent order, among which, in the course of the historical development of the leech, a division of labor was introduced, a few at the anterior end becoming specialized as light-perceiving organs, the rest either remaining in their early indifferent condition, or becoming specialized in some other direction.

The discovery that these papillæ are sense-organs might lead us to speculate on affinities of a distant and somewhat uncertain nature,

such as are supposed by the writer, in common with many others, to exist between annelid worms and vertebrates. At all events, the existence of such organs in the leech furnishes a broader basis for the discussion of the question, whether the vertebrates and annelids have been derived from a common form possessing metameric sense-organs, as was first argued by Dr. Eisig of the Naples Station. Assuming that the sense-organs of the lateral line of the vertebrate and the segmental papillæ of the leech may be traced to a common origin in some remote ancestral form, it does not follow that they should now present close structural resemblances. It is far more important to show that they possess certain general features in common. The most important of their common features is undoubtedly their metameric origin. The nerve-supply forms another feature of fundamental importance, in which, according to the interesting observations of Mr. Beard, on "the segmental sense-organs of the lateral line" (Zool. Anz., VII., Nos. 161 and 162) of the vertebrate, there is essential agreement. The developmental history of these lateral organs in the fish, where they make their first appearance as *segmental papillæ* in the strictest sense of these words, cannot at present be explained on a more satisfactory hypothesis.

The fact that the eyes of the leech are metameric sense-organs representing merely structurally improved forms of the segmental papillæ, will be placed in still clearer light by the following study of the abbreviated somites.

Hirudo and Allied Genera. — In order to arrive at satisfactory conclusions respecting the characters which distinguish the genus *Hirudo* from allied genera, we must make a thorough study of the rings and somites composing the body. The importance of this first step in a comparative study of genera will be seen as we proceed.

The obscurity that is supposed to exist in regard to the precise number of rings in the cephalic lobe and in the hind end of the body, affords no excuse for the meagre descriptions usually given of these regions; but furnishes rather an argument for describing them with the utmost care and detail. The difficulties in the way of counting the rings has been greatly overestimated. It is only necessary to adopt some method of counting that can be followed in the different genera. Some authors count the rings from the ventral side, beginning with the buccal ring (5th and 6th in my figure), and take no account of the rudimentary anal (or post-anal) ring: thus counted there would be only 95 rings, which is the number usually given for *Hirudo medicinalis* of Europe. According to another mode of counting, the rings are counted from both sides, but from two dif-

ferent points, so that the number corresponding to the dorsal half of a ring is not the same as that of the ventral half. Gratiolet, who was the first to emphasize the importance of a well-defined starting-point in counting, recommended the unconventional and extremely awkward method of beginning with the ring in which the last pair of nephridial pores is found, counting from this point forward. This is evidently an unnatural method, adopted under the persuasion that no more convenient fixed point could be found.

The simplest method, and the one least liable to confusion, seems to be that which I have followed in my diagrams, the first pair of eyes forming the starting-point. Each ring then has a definite number and precise relations, and homologous rings are easily recognized in different species. For reasons that will be made clear elsewhere by a comparison of different species, it is certain that the first three pairs of eyes in *Hirudo* mark three successive rings. Beginning with the first pair of eyes, we find the fourth and fifth pairs on the fifth and eighth rings respectively. This simple arrangement of the eyes, which is only slightly modified in the land leech (*Hæmadipsa*), holds good not only for *Hirudo*, but for *Hæmopsis*, *Aulostoma*, *Macrobdella*, and all the more closely allied genera. From the fifth pair of eyes onward, the counting is rendered more easy by the size of the rings, and by the metameric arrangement of the color-markings and the papillæ.

It is certainly very desirable that species belonging to closely related genera should be described on a common plan; and I know of no better method than the one here proposed. It is quite certain that no well-marked ring exists in front of the first pair of eyes. There are here, to be sure, in some species, obscure traces of what, in the opinion of some observers, might be regarded as one or two rings. While it is important to take note of all such evidences of rudimentary rings, it is certainly advisable, for the sake of uniformity, to discard them in counting.

Figure 1 is designed to show all the important external characters which are typical of the genus *Hirudo*. The first ring of each somite bears the segmental papillæ, and their homologues, the eyes; the papillate rings, as we may call them, show us precisely how many somites are represented between the first pair of eyes and the posterior sucker (acetabulum). The papillæ on the sucker are not usually sufficiently distinct to form a reliable guide to the number of somites represented in this part, and may therefore be left out of account. The following definition of the genus *Hirudo* will serve as a convenient standard of comparison.

Every Hirudo has 26 somites, counting from the first pair of eyes to the acetabulum: 10 of these — the first 6 and the last 4 — are abbreviated by the suppression of from 2 to 4 rings in each; and 16, lying between the first (1st p) and the last pair of nephridial pores (17th p), have each five rings. The 6 anterior somites include 13 rings, the first and second being represented each by a single ring, the third by 2 rings, and the fourth, fifth, and sixth, each by 3 rings. The 4 posterior somites embrace 9 rings (94–102), the twenty-third somite including 3 rings, and the twenty-fourth, twenty-fifth, and twenty-sixth, each 2 rings.

The first ring of each somite is marked anteriorly, by a pair of eyes; and, from the 11th ring onward, by the segmental papillæ, of which there are normally from 6 to 8 on the dorsal half of the ring, and 6 on the ventral half.

The first pair of eyes replaces a pair of median papillæ; and the remaining four pairs of eyes replace as many pairs of the inner lateral papillæ (il).

The eye-bearing rings are the 1st, 2d, 3d, 5th, and 8th.

The buccals are the 5th and 6th, which are united on the ventral side.

The post-buccals are the 7th and 8th, also united ventrally.

There are seventeen pairs of nephridial pores located in the hind edge of the ventral half of the following rings: — 13th, 18th, 23d, 28th, 33d, 38th, 43d, 48th, 53d, 58th, 63d, 68th, 73d, 78th, 83d, 88th, and 93d. Each pair is thus in the last ring of its somite. Between the first (1st p) and the last (17th p) pair there are precisely 16 complete somites (7–22 inclusive), or 80 rings (14–93 inclusive).

The male orifice lies between the 30th and 31st rings, or the 2d and 3d rings of the 10th somite. The female orifice is 5 rings behind the male, between the 35th and 36th rings, or the 2d and 3d rings of the 11th somite.

The clitellum includes the 9th, 10th, and 11th somites.

The anus lies in the 102d ring, or between this and the preceding one.

The other characters of this genus are based on internal organs, and are too well known to require repetition here.

We may now consider the abbreviated somites, and see what they have to tell us about the history and relationship of the ten-eyed leeches. We notice first of all that the abbreviation is greatest at the extreme ends, from which it is plain that it began at these points and progressed centripetally; i. e. towards the middle of the body. The first two somites have lost each 4 rings; the third, 3 rings; the fourth, fifth, and sixth, each 2 rings; making a total loss of 17 rings at this end. The twenty-third somite has lost 2 rings, and the

remaining three somites have lost 3 rings each, making a loss of 11 rings. This syncopation of 28 rings, at the two ends of the body, and at least as many more in the acetabulum, is not to be regarded as an actual loss; these rings have been sacrificed rather in the interest of the rings retained. The loss at the anterior end is correlated with a higher development of the sense-organs; at the posterior end, with a greater development of muscles. It is interesting to note that Natural Selection has played a part in deciding the fate of these rings; for the *papillate* rings have been preserved, while the non-papillate rings have been in part or wholly suppressed.

Is this suppression of rings still going on? or has it reached a limit? A closer examination of the rings in the terminal somites will show that the process of abbreviation is still advancing; and a comparison of different genera proves that its progress has not been everywhere equally rapid. The suppression of rings takes place by consolidation, two successive rings coalescing gradually. The papillate ring may unite with, or absorb, either the preceding or the following ring. In the Medicinal Leech, the 5th ring, which bears the fourth pair of eyes, is now in process of uniting with the 6th; while the 8th is absorbing the 7th. The evidence that these two rings are being swallowed up is seen, first of all, in the rings themselves; and secondly, in the different conditions which they present in different species. In *Hirudo* and several allied genera, the 6th and 7th rings are relatively narrow; and the grooves separating them from the 5th and 8th rings are obliterated on the ventral side, so that here the four rings appear as two. On the dorsal side they are still distinct, but not so deeply marked off from the 5th and 8th rings as from each other. The same process of consolidation is seen in *Hæmopis*, *Aulostoma*, and *Hæmadipsa*, but in slightly different stages. In *Macrobdella* all four rings are distinct on both sides; but the consolidation has already begun, as the grooves separating the 5th from the 6th, and the 7th from the 8th, are not so deep as the groove between the 6th and 7th, or as that between any two of the succeeding rings.

If centripetal abbreviation be the law of development, we should expect the 4th ring to disappear before the 6th and 7th. This course of events has already been realized in the land leeches (Fig. 2), in none of which is there a ring intervening between the third and fourth pairs of eyes.

Two non-papillate rings may also unite: an instance is seen in the 23d somite of *Macrobdella*, where the 2d and 3d rings (95th in Fig. 4) are wellnigh consolidated.

The elimination of rings has been carried farther in the acetabulum than in either of the posterior somites of the body. In a few species the papillæ have been well preserved on the disc; and in these cases their arrangement shows that papillate rings alone have been preserved in this region.

If the historical development of the leech has been marked by a progressive course of abbreviation, such as I have described, it is evident that an ancestral form must have existed in which the somites were more nearly alike from end to end. The embryonic development confirms this view, for in its earlier phases the somites form a chain of very nearly like parts. Later a few (7-8) of the posterior somites become constricted off and consolidated into the sucking disc. The somites at the anterior end are the first to arise, and hence the first to exhibit specialization. Among existing species, we find three in Japan which have departed less from the hypothetical ancestral form than has *Hirudo*. They agree with *Hirudo* in having 26 somites, but differ from it in having a larger number of complete somites. In each of these species we find only five abbreviated somites at the anterior end; but these five are abbreviated precisely as they are in *Hirudo*. The sixth somite embraces five rings, two more than the same somite in *Hirudo*. This difference explains other differences: for instance, the position of the first pair of nephridial pores in the 15th, instead of the 13th ring; and the position of the genital pores between the 32d and 33d, and between the 37th and 38th rings. If the difference in abbreviation is taken into account, it is seen that the nephridial pores and sexual orifices hold the same positions as in *Hirudo*. Passing to the posterior end of the body, we find that the 23d somite differs from that of *Hirudo*. In one species, *Microstoma pigrum*, this somite shows no plain evidence of abbreviation (Fig. 5); in another, *M. edentulum*, the 2d and 3d rings of this somite are often less plainly divided than the following rings; and in the third species, *M. acranulatum*, these two rings are as plainly consolidated, as in *Macrobdella* (Fig. 4). Thus one of these species has 18 complete somites; the second has 17 complete, and an 18th nearly so; the third has only 17 complete. The 24th, 25th, and 26th somites contain in each species the same number of rings as those of *Hirudo*. The 103d ring of *M. pigrum* (Fig. 5), which is the homologue of the 99th in *Hirudo*, shows signs of duplicity at its margins; and the 102d is constantly thicker than the preceding ring.

In the land leech, abbreviation has been carried farther at both ends than in *Hirudo*. The number of somites is the same in both

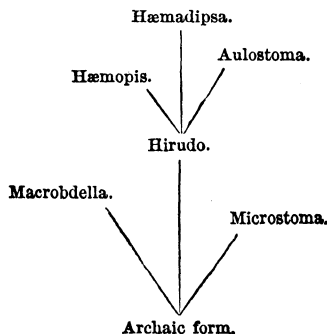
genera. The abbreviation at the anterior end is the same in both, except that the 4th ring of the aquatic leech has been dropped in the land leech. The loss of this ring brings the fourth pair of eyes into close order with the first three pairs, and the nephridial pores and sexual orifices one ring farther forward. At the posterior end (Fig. 3), we find only four rings at most to offset the last nine rings in *Hirudo*. The occurrence of segmental papillæ on each of these four rings, with perhaps the exception of the last, enables us to identify them, and to say precisely which rings have been lost since this leech abandoned its aquatic life. The rings may be identified as follows:—

93d ring (<i>Hæmadipsa</i>)	=	94th ring (<i>Hirudo</i>).
94th “	“	= 97th “
95th “	“	= 99th “
96th “	“	= 101st “

The lost rings are the 4th, 95th, 96th, 98th, 100th, and 102d.

Hæmopsis is almost an exact copy of *Hirudo* in all the details of abbreviation; and scarcely deserves to be called a distinct genus. *Aulostoma* differs from *Hirudo* by a slightly less advanced abbreviation of its 23d somite, and in some other particulars that need not be mentioned here.

The degree of abbreviation is a key to the phylogenetic relationship of species and genera. The ten-eyed leeches have descended from a common form, having twenty-six somites, of which at least eighteen were complete. Of the genera mentioned in this paper, three may be said to have branched from the archaic form, *Hirudo* representing the main branch, and *Macrobdella* and *Microstoma* diverging branches. From *Hirudo* have arisen the three secondary branches, represented by *Hæmadipsa*, *Hæmopsis*, and *Aulostoma*.



POSTSCRIPT.

In a very important paper dealing with the Hirudinea,* which came to hand only a few days before receiving the proof-sheets of the foregoing paper, Mr. Bourne calls attention to "sensory cells" found in *Hirudo medicinalis*. The following is all that is said on the subject: —

"I do not propose to do more here than draw attention to Fig. 15, from *Hirudo*, showing certain of these cells and their connections with nerve trunks. The preparation from which this is drawn was a section cut with a freezing microtome and stained in gold chloride.

"My inability to say much upon this subject is the less to be regretted since Leydig † has dealt with these simpler tactile bodies and their derivatives, the eyes, in a most detailed manner."

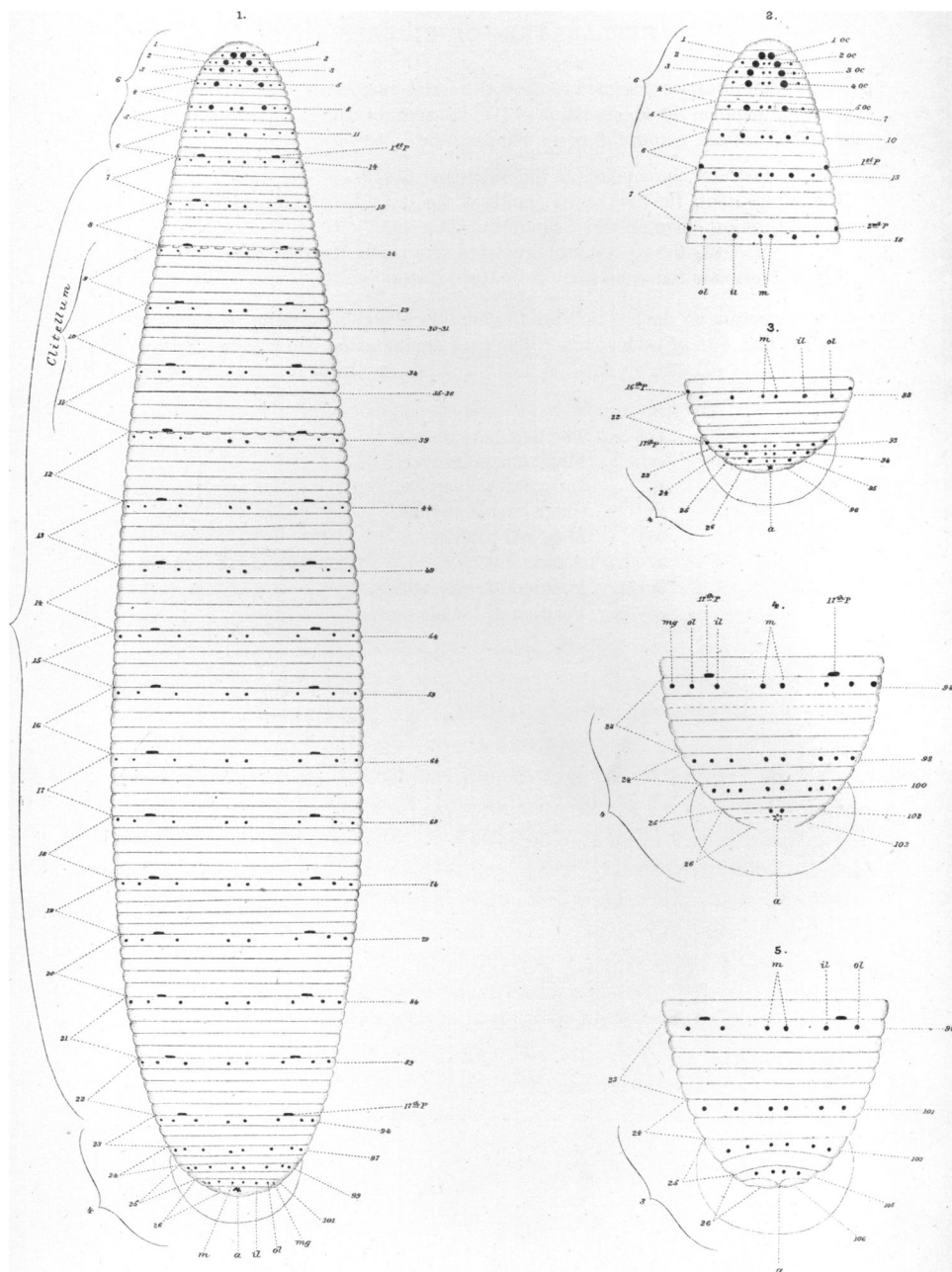
Unfortunately Mr. Bourne has not told us from what part of the leech his section was obtained, leaving it entirely uncertain whether it represents a part of a segmental papilla or one of the goblet-shaped organs on the head. As the figure shows none of those peculiar glassy cells, which are found in the eyes and segmental papillæ, it seems probable that it represents one of the simpler goblet-shaped organs which, according to Leydig, ‡ are scattered over the entire cephalic lobe.

Mr. Bourne does not enter into any discussion upon the nature of the segmental papillæ, and their serial relationship with the eyes has entirely escaped his attention. The method adopted in determining the number of somites (by reference to the number of ganglia) is of course not reliable at the ends, where a fusion of primitively distinct ganglia has taken place. I have shown that the first thirteen rings constitute six abbreviated somites, while Bourne's method enables him to recognize only eight rings and two somites in the same region.

* Quart. Journ. Mic. Sci., July, 1884, p. 434.

† Vom Bau des thierischen Körpers, 1864, and Atlas.

‡ Müll. Arch., 1861, pp. 599, 600.



EXPLANATION OF FIGURES.

These diagrams are designed to show the serial relationship of the eyes and segmental papillæ, the abbreviation of the end somites, the relative positions of the sexual orifices, nephridial pores, papillæ, &c.

Fig. 1 illustrates these points in the Medicinal Leech.

Fig. 2 represents the first seven somites of the Land Leech (*Hæmadipsa*).

Fig. 3 shows the five posterior somites of the same.

Fig. 4 represents the posterior abbreviated somites of *Macrobdella*.

Fig. 5 represents the same somites in *Microstoma*.

The numerals on the left indicate the number of somites; those on the right mark the first ring of each somite. The eyes are indicated by large black dots; the segmental papillæ, by smaller dots; and the nephridial pores, by short dashes (1st-17th *p*).

1-5 <i>oc.</i>	The five pairs of eyes.
<i>m.</i>	Median papillæ.
<i>il.</i>	Inner lateral papillæ.
<i>ol.</i>	Outer lateral papillæ.
<i>mg.</i>	Marginal papillæ.
<i>a.</i>	Anus.
30-31.	Position of male orifice.
35-36.	Position of female orifice.